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CUMENTATION PAGE

DTIC FILE COPY

1a. REPORT SECURITY CLASSIFICATION	1b. RESTRICTIVE MARKINGS
2a. SECURITY CLASSIFICATION AUTHORITY	3. DISTRIBUTION / AVAILABILITY OF REPORT
2b. DECLASSIFICATION / DOWNGRADING SCHEDULE	Approved for public release; distribution unlimited.

4. PERFORMING ORGANIZATION REPORT NUMBER(S)	5. MONITORING ORGANIZATION REPORT NUMBER(S)
	AFOSR·TR· 88-1335

DTIC ELECTED
SELECTE
DEC 16 1988
S E

6a. NAME OF PERFORMING ORGANIZATION	6b. OFFICE SYMBOL (If applicable)	7a. NAME OF MONITORING ORGANIZATION
Ctr. For Visual Science University of Rochester		AFOSR/NL

6c. ADDRESS (City, State, and ZIP Code)	7b. ADDRESS (City, State, and ZIP Code)
Rochester, NY 14627	Bldg. 410 Bolling AFB, DC 20332-6448

8a. NAME OF FUNDING / SPONSORING ORGANIZATION	8b. OFFICE SYMBOL (If applicable)	9. PROCUREMENT INSTRUMENT IDENTIFICATION NUMBER
AFOSR	NL	AFOSR-85-0019

8c. ADDRESS (City, State, and ZIP Code)	10. SOURCE OF FUNDING NUMBERS			
Bldg. 410 Bolling AFB, DC 20332-6448	PROGRAM ELEMENT NO.	PROJECT NO.	TASK NO.	WORK UNIT ACCESSION NO
	61102F	2313	A5	

11. TITLE (Include Security Classification)

Peripheral Limitations on Spatial Vision

12. PERSONAL AUTHOR(S)
Dr. Williams

13a. TYPE OF REPORT	13b. TIME COVERED	14. DATE OF REPORT (Year, Month, Day)	15. PAGE COUNT
Final	FROM 1 Dec 84 TO 31 May 88	Oct 6 1988	14

16. SUPPLEMENTARY NOTATION

17.	COSATI CODES		18. SUBJECT TERMS (Continue on reverse if necessary and identify by block number)
FIELD	GROUP	SUB-GROUP	

19. ABSTRACT (Continue on reverse if necessary and identify by block number)

➤This project employed psychophysical techniques to examine the limitation on spatial vision imposed by the first stages in the visual pathway. All the experiments capitalized on the use of laser interferometry, which allows sinusoidal gratings to be formed on an observer's retina that are immune to optical blurring. Comparisions of contrast sensitivity to such gratings with contrast sensitivity to gratings viewed under normal conditions provides an estimate of the modulation transfer function of the eye's optics. In addition, the appearance of very high frequency gratings is distroted, or aliased, byt the cone mosaic. Such moire patterns provide the basis for a number of psycholphysical techniques to assess the topography of the cone mosaic in the living eye. These measurements, accompanied by measurements of visual acuity for interference fringes clarify the relationship between cone spacing and resolution. Resolution was also measured under conditions in which only the M or L cones could detect the interference fringe. Visual acuity was little different than it was when both cone types detected the grating, showing that resolution is immune to photoreceptor loss under these circumstances. ($ \leq \epsilon $) ◀

20. DISTRIBUTION / AVAILABILITY OF ABSTRACT	21. ABSTRACT SECURITY CLASSIFICATION
☐ UNCLASSIFIED/UNLIMITED ☐ SAME AS RPT. ☐ DTIC USERS	

22a. NAME OF RESPONSIBLE INDIVIDUAL	22b. TELEPHONE (Include Area Code)	22c. OFFICE SYMBOL
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DD FORM 1473, 84 MAR   83 APR edition may be used until exhausted.   SECURITY CLASSIFICATION OF THIS PAGE
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88 12

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October 6, 1988

AFOSR·TR· 88 - 1 335

Dr. John F. Tangney, Ph.D.
AFOSR/NL, Building 410
Bolling AFB, DC 20332-6448

Dear John:

    Enclosed is the final report for my AFOSR 85-0019 grant.

Sincerely,

David R. Williams

SEE YOU AT OSA.

1 2 OCT 1988

Final Technical Report for AFOSR 85-0019
Principle Investigator: David R. Williams
Center for Visual Science
University of Rochester
Rochester, NY 14627
Project Period: 12/1/84 to 5/31/88

Project Summary:

This project employed psychophysical techniques to examine the limitations
on spatial vision imposed by the first stages in the visual pathway. All the
experiments capitalized on the use of laser interferometry, which allows
sinusoidal gratings to be formed on an observer's retina that are immune to opti-
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mate of the modulation transfer function of the eye's optics. In addition, the
appearance of very high frequency gratings is distorted, or aliased, by the cone
mosaic. Such moire patterns provide the basis for a number of psychophysical
techniques to assess the topography of the cone mosaic in the living eye. These
measurements, accompanied by measurements of visual acuity for interferfence
fringes clarify the relationship between cone spacing and resolution. Resolu-
tion was also measured under conditions in which only the M or L cones could
detect the interference fringe. Visual acuity was little different than it was
when both cone types detected the grating, showing that resolution is immune to
photoreceptor loss under these circumstances.

Research Objectives:

The objectives of the original proposal were two-fold: 1) to provide improved measurements of the optical quality of the eye, and 2) to estimate the packing geometry of the M and L cone submosaics in the living human fovea.

Status of the Research:

Six lines of investigation are outlined below that have been pursued during the AFOSR grant. They are described in turn below:

1. Optical Quality of the Human Eye.

Measurements of foveal contrast sensitivity for interference fringes obtained in my laboratory with an improved laser interferometer (Williams, 1985b) were strikingly different from those reported by Campbell and Green (1965): the more recent measurements averaged nearly an order of magnitude more sensitive at high spatial frequencies (60 cycle/deg). This finding warranted a reevaluation of Campbell and Green's estimates of the modulation transfer function of the eye, which were based on their interferometric contrast sensitivity measurements. Measurements were made of the modulation transfer function of three human eyes for 2 and 3 mm pupils, by dividing the contrast sensitivity function obtained in normal viewing by that obtained with interference fringes, as Campbell and Green had done. These new modulation transfer functions were similar to those reported by Campbell and Green (only slightly steeper), despite the large difference in interferometric contrast sensitivity. The implication is that both the coherent and incoherent contrast sensitivity functions obtained by Campbell and Green (for two subjects) revealed substantially reduced sensitivity at high frequencies compared with the 3 observers in the present study, so that the estimate of the MTF was little different. The explanation for the discrepancy in contrast sensitivity is partly procedural, but largely due to real individual differences. This was confirmed by measuring contrast sensitivity on one of Campbell and Green's original observers (Dan Green) on the improved interferometer at Rochester.

2. Color Appearance of High Frequency Interference Fringes.

Experiments performed in collaboration with Mary Hayhoe (Hayhoe and Williams, 1987) have shown that fine monochromatic gratings appear markedly desaturated compared with a uniform field of the same wavelength. Observers matched the color of a foveal uniform field to that of a monochromatic grating alternated with it. Gratings were unity contrast interference fringes with wavelengths spanning the spectrum. The matching field was a mixture of a white of adjustable intensity and an incoherent monochromatic light of adjustable intensity and wavelength. Fine gratings appear desaturated at all wavelengths, corresponding to an excitation purity of about 0.6 in the largest case. The desaturation was also seen with brief flashes of the grating and matching fields (50 msec), showing that it is not a temporal effect produced by eye movements.

Of particular interest is the observation that long wavelength gratings that stimulate only M and L cones also appear desaturated; they can only be matched by stimuli that also stimulate S cones. This excludes explanations that invoke intensive nonlinearities that differ across cone types because they would predict a shift in the color appearance of long wavelength gratings (that do not directly stimulate S cones) only along the spectrum locus in CIE space.

We proposed a second kind of explanation, in which saturation is determined by the ratio of signals in achromatic and chromatic channels, which in turn depends on spatial frequency. If the achromatic channel is spatially bandpass and the chromatic channel is low pass, the desaturation should increase with increasing spatially frequency and then decrease at still higher frequencies. Indeed, measurements show that the effect grows steadily with increasing spatial frequency, peaking at about 20 cpd, and falling off gradually at higher frequencies. In the context of this model, we estimated the spatial frequency response of the underlying chromatic and achromatic mechanisms. The estimates imply receptive fields that have centers fed by only one or two cones, with surrounds 5-6 times larger.

3. Topography of the Foveal Cone Mosaic in the Living Human Eye.

Interference fringes whose spatial frequency exceeds the resolution limit form visible moire patterns or "zebra stripes" with the foveal cone mosaic (Byram, 1944; Campbell and Green, 1965; Williams, 1985a; Williams, 1988). These moire patterns contain rich information about the topography of foveal cones in the living human eye. To confirm that the observed patterns are indeed generated by cone aliasing, I developed a model of foveal cone sampling that shows how the moire patterns should depend on the spatial frequency and orientation of an interference fringe imaged on a triangular lattice of cones. The predictions of the model were then tested and found to be consistent with the results of two psychophysical experiments.

The Moire Zero Technique: The model predicts that the moire pattern should be coarsest when the period of the interference fringe equals the spacing between cones. The intuition behind this prediction is easily grasped by considering the simplified case of a static, one-dimensional array of regular sampling elements. If the spacing between sampling elements is equal to the spacing between stripes of the grating superimposed on them, then all the elements will catch the same number of quanta. The grating will then produce the same response in the array as a uniform field would have produced. This match between grating and sampling array will be referred to as a "moire zero". This prediction was tested by asking observers to adjust the spatial frequency of the interference fringe to make the zebra stripes as coarse as possible at various retinal eccentricities within the fovea. These settings were quantitatively consistent with anatomical estimates of cone spacing across the human fovea (Osterberg, 1935; Miller, 1979; Curcio, et al, 1987). This "moire zero" technique, validated in this way, provides a psychophysical method for measuring cone spacing within 1.75 deg of the fovea.

A second prediction of the model is that, due to the 60 deg rotational symmetry characteristic of the packing of primate foveal cones (Hirsch and Hylton, 1984), the moire patterns should change from coarse to fine with every 60 deg of rotation of the interference fringe (Williams, 1988, copy in Appendix). A psychophysical experiment in which the overall spatial frequency of the moire pattern was judged as a function fringe orientation confirmed this prediction, allowing the orientation of the cone mosaic to be determined at the foveal center.

4. Additional Psychophysical Measures of Cone Spacing.

The moire zero technique for estimating cone spacing is particularly well suited to sampling arrays that are highly regular, such as the cone mosaic at the foveal center. However, the cone mosaic becomes rapidly less regular just outside the fovea, and two additional techniques were developed to estimate average

cone spacing there. These techniques, developed in collaboration with Nancy Coletta, have an advantage over the moire zero technique in that they can be implemented with a forced choice psychophysical procedure. They are described in turn below.

Orientation Reversal Technique. Coletta and Williams (1987a) observed that, in parafoveal retina, interference fringes with spatial frequencies above the resolution limit can look like two dimensional spatial noise with striations running **perpendicular** to the true orientation of the fringe. This appearance is consistent with the sampling properties of the disordered extrafoveal cone mosaic. A model constructed from the Fourier spectra of primate extrafoveal mosaics predicts that this orientation reversal should occur when the period of the interference fringe equals the average spacing between cones. Psychophysical experiment confirms this prediction, providing a measure of cone spacing in the parafovea.

Motion Reversal Technique. Another phenomenon provides a second measure of average cone spacing in extrafoveal retina. A periodic moving stimulus can appear to move in the reverse direction if it is undersampled in time, as in the case of the "wagon wheel" effect caused by an inadequate frame rate in motion pictures. Coletta and Williams (1987b) reported the spatial analog of this effect for gratings that are undersampled by the cone mosaic: high spatial frequency interference fringes, viewed in the parafovea, appear to move in the **opposite** direction from their true direction of motion. Observers named the direction of motion of vertical, unity contrast fringes whose direction was randomly determined on each trial. Percent correct fell significantly below chance performance at high spatial frequencies, indicating a reversal in the perceived direction of motion.

Insects exposed to drifting high frequency gratings show a reversed optomotor response (von Gavel, 1939; Hassenstein, 1951; Goetz, 1964) because they respond to the moire pattern produced by their photoreceptor mosaic, which moves oppositely to the original grating. If the motion reversal we have observed has the same basis, the spatial frequency at which the perceived direction of motion reverses should correspond to integral multiples of the cone Nyquist frequency. Measurements of this frequency at various eccentricities agree with anatomical and psychophysical estimates of the cone Nyquist frequency.

5. Supra-Nyquist Visual Resolution

The moire zero, orientation reversal, and motion reversal techniques all provide estimates of cone spacing that agree with each other and with the estimates from retinal anatomy in monkey and man cited earlier. This allows cone spacing and visual acuity to be compared in the same retinal locations of the same observers. It is commonly assumed that the visual resolution limit must be equal to or less than the Nyquist frequency of the cone mosaic. However, under some conditions, observers can see fine patterns at the correct orientation when viewing interference fringes with spatial frequencies that are as much as 1.5 times higher than the nominal Nyquist frequency of the underlying cone mosaic. This was confirmed with a forced choice orientation discrimination task (Williams and Coletta, 1987b).

The existence of supra-Nyquist resolution demands closer scrutiny of the sampling effects of the cone mosaic and the information that is sufficient for an observer to "resolve" a sinusoidal grating. First, sampling by the cone mosaic does not remove information about high spatial frequencies in the way that spatial filtering does. Sampling introduces ambiguity in the form of aliasing: the observed distribution of quantum catches in the mosaic is consistent with many

retinal images rather than just one. The Nyquist frequency specifies which images can be reconstructed without interference from aliasing. However, it is not a theoretical upper bound for psychophysical measures of visual resolution because the criteria for resolving sinusoidal gratings (such as orientation identification) are less stringent than the criteria specified by the sampling theorem for perfect, alias-free image reconstruction. This result is important for any attempt to relate visual resolution to the anatomical density of neural arrays in the visual system.

6. Visual Resolution and Aliasing with M and L Cone "Isolation"

One goal of the AFOSR grant was to explore aliasing effects in the separate M and L cone mosaics, with the hope of uncovering their packing arrangements in the fovea. Our strategy has been to first develop and refine of techniques applicable to the M and L cones working together, as described above, so that these techniques could be applied with more finesse to the problem of the packing arrangement of the submosaics. The progress made so far on the submosaic problem is described below.

The first question we have addressed is whether the appearance of foveal zebra stripes is affected when only a single cone submosaic (either M or L) can detect the interference fringe. Given that the zebra stripes provide a measure of cone spacing and that the total number of cones is reduced in effect by isolating a single submosaic, it might at first seem that the spatial frequency producing a moire zero would shift be lower under isolation conditions. A second question we have addressed is whether foveal resolution is reduced when either the M or L submosaic alone contributes to the task compared with conditions when both M and L cones contribute together. One view would hold that it would be: if foveal resolution is limited by cone sampling, then visual acuity for a grating that stimulates only a single cone type should be reduced as a result of the reduction in spatial sampling rate. For example, assume for simplicity that the loss of one cone type through chromatic adaptation reduces the number of effective sampling elements underlying the fringe by a factor of two. (The actual value will be somewhat more or less depending on the ratio of M to L cones). If the remaining cones were arranged in a perfectly regular lattice, the Nyquist frequency of the submosaic would be $1/\sqrt{2}$ or 71% of its value when M and L cones operate together. This simplistic application of sampling theory would then predict that visual resolution would be reduced correspondingly. As described below, our data so far are quite inconsistent with both these predictions about aliasing and resolution, which we will argue are conceptually misguided to begin with.

Chromatic adaptation was used to attempt to isolate M or L cones in the manner of Green (1968). Measurements were made for three kinds of interference fringe stimuli: 1) those of equal contrast for M and L cones produced by superimposing either a 488 nm or a 633 nm fringe on a background of the same wavelength, 2) fringes that favored M cone grating detection in which a unity contrast 488 nm grating was superimposed on a 660 nm uniform adapting field, and 3) fringes that favored L cone grating detection in which a unity contrast 633 nm grating was superimposed on a 460 nm background. The observer made two settings for each of these conditions of chromatic adaptation: 1) he adjusted the spatial frequency of the fringe to his resolution limit defined as the highest spatial frequency at which he could perceive fine stripes at the appropriate orientation, and 2) He adjusted the spatial frequency of the interference fringe to produce the coarsest zebra stripes at the foveal center (moire zero).

The mean settings for both these tasks are plotted in Fig. 1. The abscissa is an index of the cone isolation achieved by the three adaptation conditions, where

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0 indicates perfect M cone isolation, 1 indicates perfect L cone isolation, and 0.5 indicates equal contrasts in both M and L cones. The contrasts in the M and L cones for each of these stimuli were calculated using Smith and Pokorny fundamentals (Boynton, 1979). The most extreme adaptation conditions used produced roughly 30% contrast in the favored cone type, and about 3% in the unfavored cone type. These conditions were chosen, based on the results of contrast sensitivity measurements, so that both fringes near the resolution limit and zebra stripes would be above contrast threshold for the favored cone mechanism, but well below threshold for the unfavored cone mechanism. The results show that neither resolution nor the moire zero depend on the ratio of contrasts in the two cone types, even when the ratio approaches a factor of 10. Furthermore, the observer could detect no obvious subjective difference between the zebra stripes seen when both cone types operating together and when one or the other cone type was strongly favored.
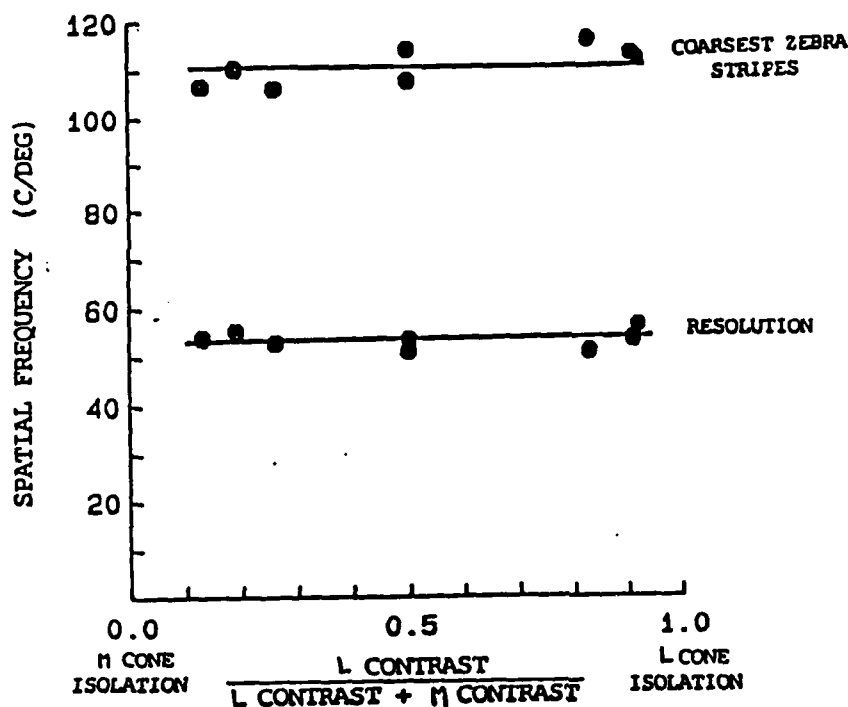

Fig. 1

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Why shouldn't foveal resolution decrease when only one submosaic is operating? The logic that leads to the prediction of a resolution loss under chromatic adaptation rests on the assumption that the remaining submosaic is perfectly regular. This is unlikely to be true, and we have previously shown that, under some conditions, observers can reliably identify the orientation of a grating even when its spatial frequency exceeds the Nyquist limit, calculated in this way, by 50%. That is, the invariance of visual resolution with chromatic adaptation is consistent with supra-Nyquist resolution observed in the parafovea (Williams and Coletta, 1987). Despite the removal of sampling elements by chromatic adaptation, there are apparently sufficient samples remaining to provide the observer with enough information to recognize a grating as a grating.

Unfortunately, this conclusion rests on the assumption that the chromatic adaptation technique succeeded in "isolating" a single cone mechanism. which is not is not immune to criticism.

Why doesn't the moire zero change when only one submosaic is operating? The moire zero should not change because the removal of sampling elements from a mosaic, in either a random or regular fashion, does not eliminate the periodicity in the mosaic that is responsible for the moire zero. This fact can be understood by considering Fig. 2. Panel A, on the left, shows shows a regular triangular lattice sampling a grating whose period nearly equals the sample spacing. The low frequency diagonal grating is the resulting moire or alias. On the right, 2/3 of the samples from the original array have been removed in random fashion. Clearly, the moire is unaffected. The lower panel (B) shows that this is true even if the removal of cones in nonrandom. In this case, on the right, only every third row of receptors have been retained, yet the moire is the same. So there is in fact no theoretical expectation that the spatial frequency yielding the coarsest zebra stripes should change when one submosaic is effectively removed.

This does not imply that there are no differences in the aliasing effects predicted for a complete mosaic and the submosaics that comprise them. For example, the submosaic on the lower right has a Nyquist frequency for horizontal gratings that is only a third that of the complete mosaic. This implies that there will be a second moire zero for the submosaic at a third the frequency of the moire zero shared by both mosaics. That is, regular submosaics should show additional moire effects at low frequencies over and above those seen with the complete sampling array. Completely random submosaics, on the other hand, would produce 2-dimensional aliasing noise at all spatial frequencies that would not be present with the complete mosaic (Ahumada, 1986).
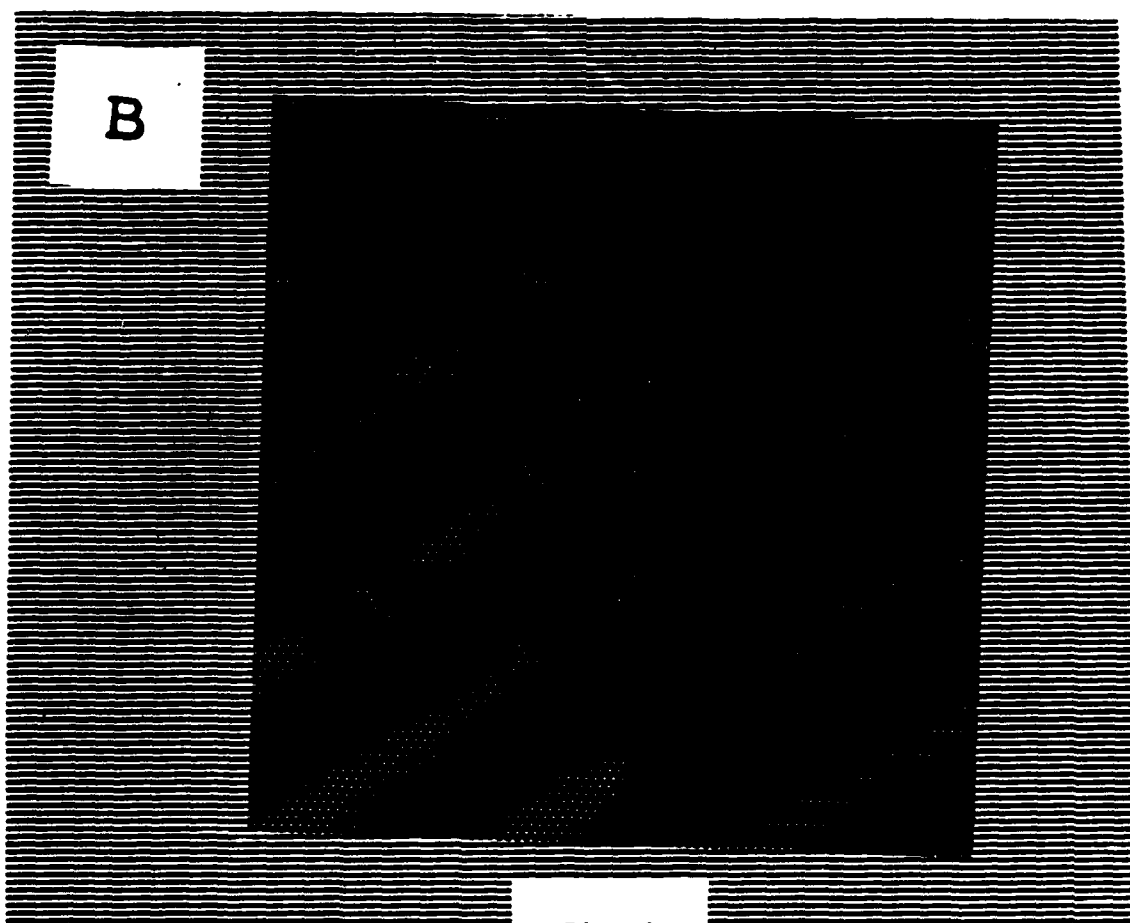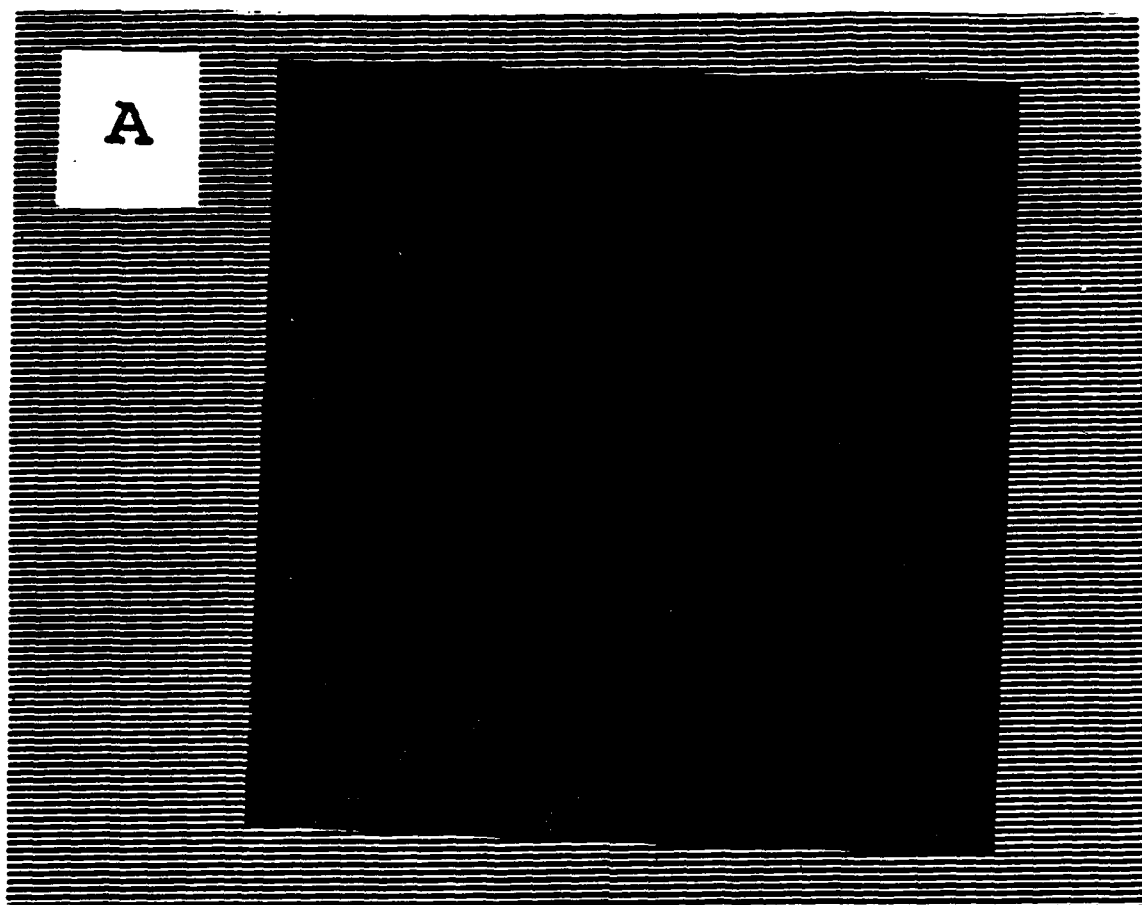
Fig. 2

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Coletta, N.J. and Williams, D.R. Consequences of cone sampling for motion perception. To be submitted to *Vision Res.*

Macleod, D.I.A., Williams, D.R., and Makous, W.M. Difference frequency gratings above the resolution limit. To be submitted to *Vision Res.*

Makous, W.M., MacLeod, D.I.A., and Williams, D.R. A nonlinearity in early vision. To be submitted to *Vision Res.*

Tiana, C., Williams, D.R., and Coletta, N.J. Model of the motion reversal phenomenon. To be submitted to *Vision Res.*

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Donald I.A. MacLeod, Full Professor, UC, San Diego

INTERACTIONS:

COLLOQUIA:

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MacLeod, D.I.A., Williams, D.R., and Makous, W. Difference frequency gratings above the resolution limit. Association for Research in Vision and Ophthalmology, 1985.

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INVENTIONS: None.

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